

RESTING HABITAT SELECTION BY FISHERS IN CALIFORNIA

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Abstract: We studied the resting habitat ecology of fishers (*Martes pennanti*) in 2 disjunct populations in California, USA: the northwestern coastal mountains (hereafter, Coastal) and the southern Sierra Nevada (hereafter, Sierra). We described resting structures and compared features surrounding resting structures (the resting site) with those at randomly selected sites that also were centered on a large structure. We developed Resource Selection Functions (RSFs) using logistic regression to model selection of resting sites within home ranges, and we evaluated alternative models using an information-theoretic approach. Forty-five fishers were radiomarked, resulting in 599 resting locations. Standing trees (live and dead) were the most common resting structures, with California black oak (*Quercus kelloggii*) and Douglas-fir (*Pseudotsuga menziesii*) the most frequent species in the Sierra and Coastal study areas, respectively. Resting structures were among the largest diameter trees available, averaging 117.3 ± 45.2 (mean $\pm$ SE) cm for live conifers, 119.8 ± 45.3 for conifer snags, and 69.0 ± 24.7 for hardwoods. Females used cavity structures more often than males, while males used platform structures significantly more than females. The diversity of types and sizes of rest structures used by males suggested that males were less selective than females. In the Sierra study area, where surface water was less common, we found almost twice as many resting sites as random points within 100 m of water. Multivariate regression analysis resulted in the selection of RSFs for 4 subsets of the data: all individuals, Sierra only, Coastal only, and females only. The top model for the combined analysis indicated that fishers in California select sites for resting with a combination of dense canopies, large maximum tree sizes, and steep slopes. In the Sierra study area, the presence of nearby water and the contribution of hardwoods were more important model parameters than in the Coastal area, where the presence of large conifer snags was an important predictor. Based on our results, managers can maintain resting habitat for fishers by favoring the retention of large trees and the recruitment of trees that achieve the largest sizes. Maintaining dense canopy in the vicinity of large trees, especially if structural diversity is increased, will improve the attractiveness of these large trees to fishers.

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The fisher has been extirpated from extensive regions of its historical range in the Pacific states (Gibilisco 1994, Powell and Zielinski 1994, Aubry and Lewis 2003). In California, the fisher appears to occupy less than half of the range it did in the early 1900s, and the species' range is divided into 2 remnants separated by approximately 400 km (Fig. 1; Zielinski et al. 1995). This separation is almost 4 times the species' maximum recorded dispersal distance (York 1996). Fishers occur in

mature, structurally complex, conifer–hardwood forests and are described as being among the most habitat-specialized mammals in North America (Harris et al. 1982, Buskirk and Powell 1994). Few studies, however, have attempted to quantify the habitats selected by fishers in the western United States.

California is unique among western states in that fishers have persisted since before European settlement, and the state has received no reintroductions from elsewhere. The fisher population in northwestern California has been the subject of several previous studies (Buck et al. 1994, Seglund 1995, Klug 1996, Dark 1997), and, although the fisher population probably is the largest in the western United States, it is isolated from other populations (Powell and Zielinski 1994, Aubry and Lewis 2003). The ecology of fishers in the Sierra Nevada has never been formally

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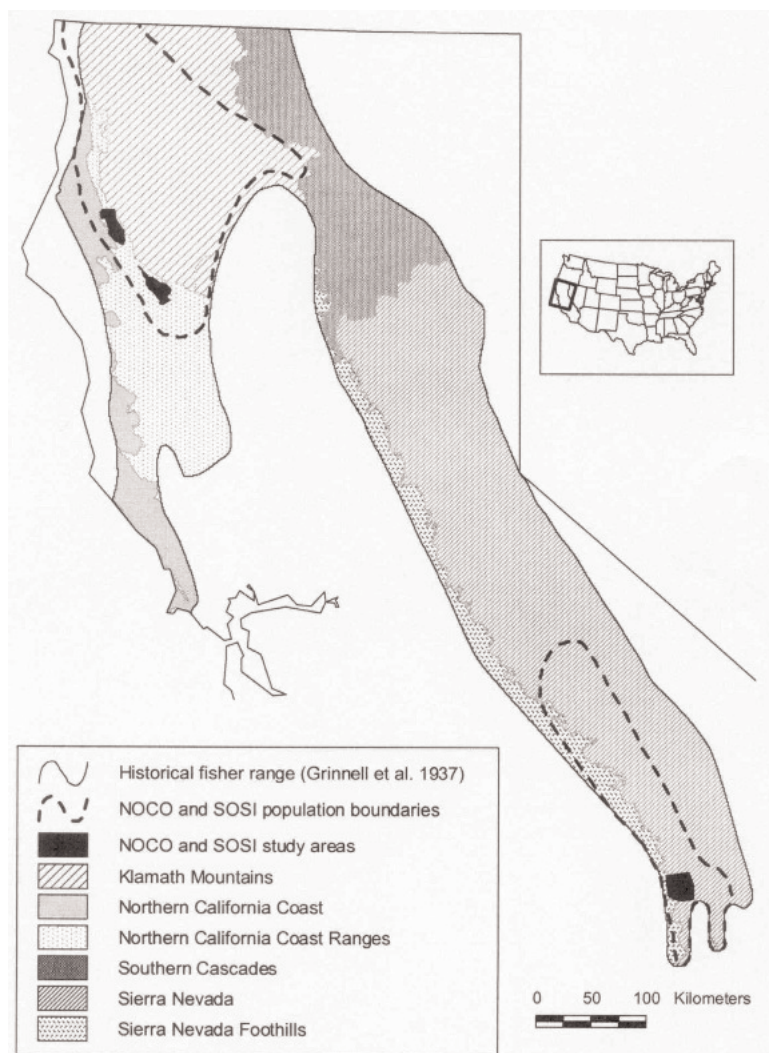


Fig. 1. North Coast (Coastal) and Southern Sierra (Sierra) study areas relative to the approximate boundaries of existing fisher populations and Ecological Sections (Bailey 1994) within the historical range of the fisher in California, USA (Grinnell et al. 1937).

studied. Fishers in the Sierra Nevada occupy an environment that differs from the mesic forests of the Pacific Northwest and Rocky Mountains and the moist, mixed-hardwood-conifer forests of the Great Lake states and northeastern North America. Fishers in the Sierra Nevada also are at the southernmost extent of their North American range, which probably accounts for their reduced genetic diversity (Drew et al. 2003).

Fishers have at least 1 daily resting bout and often use a different resting structure for each occasion (Kilpatrick and Rego 1994). Large, live trees with hollows, snags, logs, stumps, "witches brooms"

(Bull et al. 1997), squirrel and raptor nests, brush piles, rock piles, and holes in the ground have been reported as resting sites during various seasons (Grinnell et al. 1937; deVos 1952; Coulter 1966; Powell 1977, 1993; Arthur et al. 1989; Kilpatrick and Rego 1994). Resting locations protect forest mustelids from unfavorable weather and predators (Buskirk et al. 1989, Kilpatrick and Rego 1994, Zalewski 1997, Wilbert et al. 2000); thus, choosing a resting site may be among the most important choices made by fishers outside the breeding season. Previous work indicates that fishers and the congeneric American marten (*Martes americana*) are most selective about choosing natal den and resting sites and the least selective about foraging locations (Kelly 1977, Burnett 1981, Arthur et al. 1989, Jones and Garton 1994, Powell 1994, Schumacher 1999). This suggests that resting and denning sites may be the most limiting habitat element across fisher ranges.

The number and type of resting structures available as habitat are directly related to the processes of forest growth, disturbance, and resource extraction. The forests of the western United States have undergone significant changes in the latter half of the twentieth century. Logging and fire have resulted in estimates of loss of the late-successional forests in the Pacific States that range from 60 to 85% (Morrison et al. 1991, U.S. Forest Service and U.S. Department of the Interior 1993, Franklin and Fites-Kaufman 1996, Beardsley et al. 1999). The use by fishers of large trees and snags and the association of fishers with dense for-

est cover (Carroll et al. 1999, Weir and Harestad 2003) would appear to make fishers especially vulnerable to these changes in forest ecosystems.

Our goal was to characterize the resting habitat features selected by fishers in California and to contrast the resting habitat features selected by fishers in the northern Coast Range and those in the southern Sierra Nevada. This information will enable managers and researchers to tailor their recommendations about the habitat needs of fishers to specific regions of interest and to develop methods to assess habitat conditions in each area. New information about fisher resting-site selection in California will also shed light on the perceived differences in the use of mature and old-forest stands in western and eastern North America. Research in the western United States indicates that fishers are associated with extensive mature conifer forests and that large woody elements of these forests are requirements (e.g., Harris et al. 1982, Buck et al. 1994, Jones 1991, Weir and Harestad 2003). In contrast, research in the north-eastern and midwestern United States suggests that mid-successional, mixed broad-leaved and coniferous forests provide suitable fisher habitat (Arthur et al. 1989, Buskirk and Powell 1994, Krohn 1994).

STUDY AREAS

Our 2 study areas (Fig. 1) are in the Humid Temperate Domain, Mediterranean Division, and the Sierran Steppe-Mixed Forest Coniferous Forest Province (Bailey 1994). The Sierra study area lies within the Sierra Nevada and the Sierra Nevada Foothills Sections, while the Coastal study area is within the Northern California Coast Ranges Section (Bailey 1994). Weather patterns in both areas are typical of California's Mediterranean climate: summers are hot and dry, while winters are cool and moist, with precipitation often falling as snow in the higher elevations. Despite these similarities, differences in proximity to the Pacific Ocean and latitude (Fig. 1) have resulted in important differences between the areas. The Coastal study area was located within 50 km of the Pacific Ocean and received more precipitation, resulting in dense and continuous forest cover; the southerly location and lower precipitation in the Sierra area have resulted in a landscape with greater heterogeneity.

The Coastal study area was in Humboldt and Trinity counties on approximately 400 km² of the Six Rivers and Shasta-Trinity national forests. We collected data May 1993–September 1997. The study area included 2 subareas: the northern Pilot Creek and the southern Cedar Gap (Fig. 1).

Topography in the Pilot Creek area was dominated by South Fork Mountain, a 72-km-long continuous ridge joining the 2 subareas. Elevations ranged from approximately 600 to 1,800 m, and the area was vegetated by stands of Douglas-fir, white fir (*Abies concolor*), Oregon white oak (*Quercus garryana*), tanoak (*Lithocarpus densiflora*), red fir (*A. magnifica*), and dry grasslands, with a minor component of California black oak, canyon live oak (*Q. chrysolepis*), incense cedar (*Calocedrus decurrens*), and ponderosa pine (*Pinus ponderosa*; U.S. Forest Service 1995, Jimerson et al. 1996).

The Sierra study was conducted on 300 km² in the Sequoia National Forest in Tulare County (Fig. 1). Data were collected during April 1994–October 1996. Elevations ranged from approximately 800 m in the west-slope foothills to over 3,000 m at the southern Sierra Nevada's Great Western Divide. The primary vegetation types (Mayer and Laudenslayer 1988) were Sierran mixed conifer, ponderosa pine, red fir, montane hardwood, and various chaparral types. Lodgepole pine (*Pinus contorta*), Jeffrey pine (*P. jeffreyi*), and grassland/meadow types composed a small minority of the area. Stands characterized by trees averaging >30-cm diameter at breast height (dbh) occurred over 56% of the area; stands with trees averaging >61-cm dbh occurred over 10% of the area. Clearcutting has been the traditional silvicultural method in the Coastal study area (U.S. Forest Service and U.S. Department of the Interior 1993), whereas individual-tree selection harvest is more common in the southern Sierra Nevada (McKelvey and Johnson 1992).

METHODS

Animal Capture and Handling

We initially trapped fishers in areas where they had been detected at track plate survey stations (Zielinski and Kucera 1995) and throughout our study area where habitat appeared suitable. We used Tomahawk live traps (model 207, Tomahawk Live Trap Company, Tomahawk, Wisconsin, USA) modified with a plywood cubby box attached to the closed end to provide shelter. We baited traps with chicken and a commercial scent lure (M & M Fur Company, Bridgewater, South Dakota, USA), and we checked traps daily. To prevent detaining females near the time of parturition and early stages of kit rearing, we did not trap between late March and early May. We conducted additional trapping to replace failed radiotransmitters or to capture new animals.

We restrained fishers in a metal handling cone and sedated them with a ketamine hydrochloride and Diazepam mixture (10 mL ketamine/5 mL Diazepam); animals typically received 0.15–0.20 mL/kg body mass. Once immobilized, animals were sexed, measured, weighed, ear-tagged, and photographed. Fishers were fitted with Telonics (Mesa, Arizona, USA) model 80 radiotransmitters for females and model 125 radiotransmitters for males.

Animal Relocation

Radiomarked Animals, Walk-in Surveys.—Using hand-held receivers and antennas, we attempted to relocate all radiomarked fishers at least once per week using walk-in surveys (direct approaches to attempt to visually locate resting animals). We conducted walk-in surveys by following the signal of animals whose radiotransmission indicated that they were inactive for at least 30 min prior to the start our survey. We categorized 14 resting-structure types: cavity in live tree, broken top in live tree, unknown location in live tree, cavity in snag, broken top in snag, unknown location in snag, stump, animal nest, mistletoe and witches brooms (Bull et al. 1997), logs, coarse woody debris pile, subnivean site, ground burrow, and rock pile. When the radio signal confirmed the location of a fisher to a particular live tree or snag with conspicuous cavities, and the animal was unlikely to be hidden in dense canopy, we assumed that the fisher was occupying a cavity in the tree. When our search resulted in the visual confirmation of a resting fisher, we were able to relate the characteristics of the signal to the distance from the animal. This experience indicated that our error was usually <10-m horizontal distance. Often the error was less because numerous sites could be excluded from consideration since all possible resting locations were visible. Snow restricted access to the Coastal study area from the ground during the winter, so a smaller proportion of locations were collected during this time from the Coastal than from the Sierra area. Natal and maternal dens were identified when the pattern of resting-structure use by a female changed from multiple sites to 1 site during the early spring or when kits were observed with an adult. We did not include structures known to be used as natal and maternal dens in the resting-structure or resting-site analysis.

Habitat Sampling

We developed habitat sampling protocols to collect data on (1) characteristics reported in the

literature to be important to fishers, (2) features that differed between the 2 study areas, and (3) habitat conditions that may be unique to fishers in California. We grouped variables into 6 families: topographic, vegetation cover type, tree abundance, tree size, ground cover, and canopy closure.

Sampling Used Resources.—When we located resting animals in live trees and snags, we recorded tree species, dbh (1.4 m), estimated height (m), estimated height of resting structure (m), and condition class (Maser et al. 1979). For logs, we recorded the species, estimated maximum diameter (cm), minimum diameter (cm), and total length (m), measured log aspect, and assigned the log a decay class (Maser et al. 1979). The species of standing trees used as resting structures were aggregated based on growth characteristics and functional form. Due to the absence of Douglas-fir in the Sierra area, this species was considered a unique category for the Coastal area. Common to both study areas were the following groups: hardwoods (California black oak, interior [*Quercus wislizenii*] and canyon live oak, madrone [*Arbutus menziesii*], chinquapin [*Chrysolepis chrysophylla*], and tanoak), pines (sugar [*Pinus lambertiana*], ponderosa, and Jeffrey), true firs (red and white fir), and other conifers (incense cedar, unknown conifers, and, for the Sierra area, giant sequoia [*Sequoiadendron giganteum*]).

We described habitat at the resting site as the vegetation and landscape characteristics in the immediate vicinity of the resting structure. The resting structure was plot center for these measurements. We recorded aspect using a compass and percent slope by averaging the uphill and downhill clinometer recordings. Topographical position of the resting structure was categorized as ridge top, mid-slope, or drainage bottom, and we estimated the distance to water if it was within 100 m of the resting structure. One-hundred meters was the distance over which the watercourse appeared to most directly influence the forest structure and composition. For sites located during the snow season, we recorded the snow depth surrounding the resting site by averaging 4 measurements 10 m from the structure in each cardinal direction. At both study sites, we applied the California Wildlife Habitat Relationships (CWHR) system to assign a habitat type, size class, and canopy cover to the area surrounding the resting structure (Mayer and Laudenslayer 1988).

We conducted variable radius sampling using a 20-factor prism to describe aspects of forest structure and composition included in the tree-abun-

dance and tree-size variable families. For all live trees and snags in the prism sample, we recorded the species and dbh (minimum = 16 cm), and we estimated height and condition class using the same categories as for resting structures. We used line intercept sampling to describe ground-level attributes. Two 25-m line intercept transects were placed perpendicular to each other; transect placement was based on a random azimuth. For every 1-m increment, we measured cover by small trees (<7-cm dbh), shrubs, and coarse woody debris. For each meter interval with shrub cover, we recorded shrub species and visually estimated height. Coarse woody debris included all dead and down woody material with estimated minimum diameter ≥ 15 cm. For all dead and down material >30-cm minimum diameter, we estimated total length, maximum and minimum diameter, and decay class (Maser et al. 1979). Percent ground cover by litter, rock, snow, and herbaceous vegetation was recorded at every other 1-m interval using a 30 $\times$ 30-cm cover square. At the end of each transect and at plot center (the resting structure), we used a spherical densiometer to estimate total percent cover of overhead vegetation. Most habitat features were sampled within 2 weeks of locating a resting structure.

Sampling Available Resources.—We developed a set of criteria to select individuals for which we had collected sufficient information to include in resource-selection analysis. We selected “focal” animals for analysis that had been (1) monitored for at least 10 months; (2) relocated at a minimum of 10 resting locations; and (3) relocated, using any location type, a minimum of 20 times. For these animals, we calculated 100% Minimum Convex Polygon (MCP) home-range estimates using program CALHOME (Kie et al. 1996). We used a Geographic Information System (GIS) to generate 20 random Universal Transverse Mercator coordinates within each focal animal’s home range. To sample available habitat, we oriented as closely as possible to GIS-generated random coordinates, and we then selected a random azimuth and distance (10–50 m) to locate a starting point. We used a modified T-square sampling approach (Besag and Gleaves 1973) to locate a structure-centered random point. First, we searched >12.5 m from the starting point for the nearest tree or log with size characteristics similar to those of trees and logs used by fishers at each study area. A circle was drawn with a radius equal to the distance from the starting point to the first structure. The structure selected as the center of

the random plot was the closest structure that met the minimum size requirements that was also outside a line tangent to the circle.

For the Sierra study area, conifers were candidate structure points if >76-cm dbh, hardwoods if >42-cm dbh, and logs if >80-cm maximum diameter. For the Coastal study area, minimum sizes were conifers >80-cm dbh, hardwoods >56-cm dbh, and logs >62-cm diameter. The final structure category was conifers with conspicuous platforms (e.g., accumulation of litter on branches), which were eligible if they exceeded 30-cm dbh. Platforms had to be capable of supporting a resting fisher and of the minimum diameter criterion. Each minimum was 1 standard deviation less than the mean for resting sites of the corresponding type.

We collected vegetation data at random sites during May–October 1996 on the Sierra study area and during May–September 1997 on the Coastal study area. We collected habitat data at random sites using a similar protocol as was used at resting sites. Identical methods were used for 5 of 6 variable families. Line-intercept transects were used only to tally the number of logs at random sites, rather than to record the total amount of intercept, and transect distance was paced instead of measured. Shrub cover was estimated by visual observation.

Because giant sequoias are so much larger than any other tree species, and they only occur on the Sierra area, they would affect some variables we wished to compare between study areas. Eighty-three resting and random sites included ≥ 1 giant sequoia. Including giant sequoias in the estimation of 6 tree-diameter variables (total, conifer, maximum, standard deviation, quadratic mean, quadratic mean of conifer) significantly increased each variable ($t > 9.0$ and $P < 0.001$ for all comparisons). We excluded giant sequoias from the calculations of dbh but retained them to calculate basal area because of their influence on stand density and cover.

Rest-structure Analysis

We aggregated the 14 structure types into 5 functional groups: live trees (cavities, broken tops, unknown locations in live trees); snags (cavities, broken tops, stumps, unknown locations in dead trees); platforms (nests, mistletoe growths, witch’s brooms); logs (individual logs and coarse woody debris piles); and ground cavities (subnivean sites, ground burrows, rock piles). These classes were further aggregated to the coarse categories of

standing trees (live and dead) and ground structures (logs and ground cavities). Comparisons of resting structures between sexes and study areas were conducted by calculating frequency distributions and using chi-square statistics.

Habitat-selection Analysis

Comparisons of used and available resources are standard in habitat-selection studies, but few have examined the potential influence that physical characteristics of the used location may have on surrounding habitat. When the used structure represents an uncommon feature of the habitat (e.g., large tree or snag), the structure itself can influence surrounding habitat characteristics (e.g., Sieg and Becker 1990, Jones 2001). Because fishers often rest in large trees (Powell and Zielinski 1994), the presence of these features can influence the surrounding vegetation. We examined habitat selection at the rest site by comparing used sites to random sites conditioned on the presence of a large central woody structure (e.g., Edwards and Collopy 1988).

We collected a sample of used sites (resting locations) and available sites (randomly selected locations) from individual animals, and we used RSF analysis (Manly et al. 1993) to identify characteristics that distinguished sites where fishers rested from available sites. The analyses were retrospective in that a sample of use data was collected and a second, independent sample of available resources was collected later. The estimated RSFs took the form:

$$W(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \dots \beta_n x_n),$$

where $W(x)$ is the relative probability of resource use for the given combination of covariates (X_i), and slopes (β_i) are estimated using maximum-likelihood methods. The data were analyzed using logistic regression (SAS Institute 1990). The intercept in the RSF was treated as a nuisance parameter and excluded from the logistic model (McCullagh and Nelder 1989).

Habitat Characteristics at Used and Available Sites.—After developing a set of over 100 variables to describe habitat surrounding used and available sites, we reduced the pool of potential variables using the following criteria: field repeatability, the magnitude of variances, multicollinearity, univariate comparisons of mean values, and those that the literature suggested had biological and management relevance. Throughout the process, we placed greater emphasis on retaining physiog-

nostic rather than floristic variables, consistent with the conclusions of previous habitat studies on fishers and martens (Buskirk and Powell 1994).

For a subset of continuous variables, we calculated descriptive statistics for resting and random sites. We used *t*-tests, controlling the Type I error rate for the number of comparisons ($\alpha = 0.05/\text{no. of comparisons}$), to conduct univariate tests of differences between the mean value of a variable at resting sites and at random sites. For continuous variables, the means were generated from the mean values for a site type for individual focal animals. Differences between site types for categorical variables were analyzed by pooling all site types for all individuals and evaluated using either contingency tables or Fisher's exact test (Zar 1984). We used the results of these analyses to describe habitat and to guide variable selection for RSF analysis (Manly et al. 1993).

Variable Reduction, Data Pooling, and Resource Selection Functions.—We conducted univariate logistic regression for each variable to assess the potential importance of individual variables in distinguishing used from available sites. Variables with significant slopes ($P < 0.25$ threshold; Hosmer and Lemeshow 1989) were retained. We developed 4 multivariate RSFs that represented 3 levels of data aggregation: (1) all individuals—referred to as the Fisher model; (2) all individuals within each study area—referred to as the Coastal and Sierra models; (3) all females—referred to as the Female models. We were unable to monitor sufficient males to develop a RSF for this sex.

Development of the RSF models involved several steps. First, to identify candidate models for each of the 4 analyses, we conducted best subsets logistic regressions (Hosmer and Lemeshow 1989), selecting the best 3 logistic models with 3–8 predictor variables (i.e., the best 3 models using 3 predictor variables, the best 3 models using 4 predictor variables, etc.). For this analysis, data were pooled across individuals prior to model fitting. This resulted in a total of 21 candidate models for each of the 4 selection analyses. We evaluated models that were constructed only from the smallest subset of variables that we considered biologically important for fishers, rather than exploring all possible subsets of variable combinations (Anderson and Burnham 2002).

Second, for each of the 21 candidate models per selection analysis, we fitted each model to each individual focal fisher and calculated Akaike's Information Criterion adjusted for small sample size (AIC_c; Akaike 1973, Burnham and

Table 1. Mean (SD) values for the number of resting sites and habitat plots sampled per individual fisher for each season. Data are summarized separately for each study area (Coastal: Six Rivers National Forest, California, USA, May 1993–Sep 1997; Sierra: Sequoia National Forest, California, USA, Apr 1994–Oct 1996) and for males and females. The total number of sites is summarized at the bottom of table where data from focal animals are distinguished from non-focal animals. Resting sites reused by different individuals, or by the same individual at least 7 days apart, contribute to totals. Summer is the period from 16 Apr to 31 Oct, and winter is the period from 1 Nov to 15 Apr.

Study area	Sex	Resting sites		Habitat plots	
		Summer	Winter	Summer	Winter
Coastal	Both	14.4 (8.7)	2.7 (1.8)	13.1 (5.5)	2.6 (1.7)
	Females	11.7 (4.7)	2.6 (2.0)	11.7 (4.7)	2.6 (2.0)
	Males	24.0 (15.6)	3.0 (1.4)	18.0 (7.1)	2.5 (0.7)
Sierra	Both	20.6 (14.0)	7.7 (7.5)	15.8 (10.7)	6.2 (5.7)
	Females	24.8 (15.6)	9.4 (8.7)	19.3 (11.6)	7.4 (6.5)
	Males	12.3 (2.5)	4.3 (2.6)	9.0 (2.9)	3.8 (3.1)
Both	Both	18.0 (12.1)	5.5 (6.2)	14.7 (8.8)	4.6 (4.7)
	Females	18.7 (13.3)	6.2 (7.2)	15.7 (9.6)	4.8 (5.4)
	Males	16.2 (9.4)	3.8 (2.2)	12.0 (6.1)	3.3 (2.5)
Total resting sites and habitat plots					
Focal		377	116	308	97
Non-focal		93	13	60	9
Combined		470	129	368	106

Anderson 2002). For each candidate model, we summed AIC_c values across fishers and calculated Akaike weights. We identified top models based on Akaike weights, and if the model with the lowest AIC_c value also accounted for >90% of the Akaike weights, it was selected as the best model. Otherwise, we identified top models whose cumulative Akaike weights were >0.90 (Burnham and Anderson 2002).

Finally, we estimated parameters for each RSF model. For selection analyses where a single top model was identified (i.e., Akaike weight > 0.90), we calculated a weighted average of parameter estimates from the top model for each fisher, where the weight was the inverse of the standard error of the parameter (i.e., precise estimates were weighted more heavily than less precise estimates). For selection analyses that did not identify a single top model, we calculated the model-weighted parameter estimates for each fisher using renormalized Akaike weights to estimate parameters and their unconditional standard errors (Burnham and Anderson 2002). Final RSF parameter estimates were calculated as above but were weighted by the inverse of the unconditional sampling variance.

We eliminated models for some RSF analyses when variables were included for which complete or quasi-complete separation of data points existed. This form of overdispersion occurred when a site type lacked representation from 1 or the other state of a nominal scale variable (e.g., presence/absence of large snags, presence/absence

of water <100 m from site). Under these conditions, maximum likelihood parameter estimates for some or all variables did not exist.

Assessing Model Performance.—We examined the performance of final models using data from animals that were not included in developing the models (i.e., non-focal animals and data from focal animals that were excluded due to the problem of complete separation of data points). Relative predicted probabilities were calculated using the

appropriate final RSF, and data for all observations were rescaled such that the maximum relative predicted probability of use assumed a value of 1. We did not attempt to classify test sites as used or unused and instead examined the distribution of relative probabilities for used and random sites.

RESULTS

Animal Capture and Relocation

We radiomarked 45 fishers, 23 (8 M, 15 F) on the Sierra and 22 (8 M, 14 F) on the Coastal study area. We located resting fishers 397 times at 338 structures on the Sierra study area and 202 times at 195 structures on the Coastal study area. Of the radiomarked animals, 12 (4 M, 8 F) on the Sierra study area and 9 (2 M, 7 F) on the Coastal study area met our criteria as focal animals. Resting-site relocation was less successful during the snow season than the snow-free season (Table 1). The number of resting sites located for focal individuals ranged from 10 to 69 with a mean of 23.5 per animal.

Resting-structure Use

Thirty-six fishers (13 M, 23 F) used resting structures on 599 occasions. This includes 66 occasions when an individual reused a structure it had used previously (excluding reuses of natal or maternal dens). We observed fishers (visual or audible) at 191 of the 599 occasions. Unknown locations in live trees comprised 63.4 and 34.6% of the live-tree category in Coastal and Sierra, respectively. Live trees constituted 46.4% of the resting structures

used by fishers. Douglas-fir accounted for 65.6% of all resting sites located in the Coastal study area. Hardwoods comprised nearly 45% of all resting locations, and California black oak was the predominant species (approx 85% of hardwoods species used). Black oaks produce cavities that were used regularly for resting by fishers in both areas, but they were used more frequently in the Sierra (37.5% of all resting structures) than the Coastal area (10.9% of resting structures). The average size of resting structures, within type, was similar for all sex $\times$ study area combinations (Appendix A). Live conifers and snags were the largest structures used ($\bar{x}$ = 117.3-cm dbh, for live conifers; $\bar{x}$ = 119.8-cm dbh for conifer snags; Appendix A). Resting-structure reuse was low overall, but higher in the Sierra (55 reuses, 13.8%) than in the Coastal (7 reuses, 3.5%) study area.

The sexes did not use all structure types similarly (χ^2 = 31.86, P < 0.001), presumably due to the greater use of platforms by males (16.8 vs. 8.3%) and the more frequent use of snags by females (31.7 vs. 18.0%). Study area also significantly affected the distribution of resting-structure use (χ^2 = 22.93, P < 0.001), due primarily to the differential use of platforms (Coastal: 18.3%, Sierra: 6.8%). Males used platforms significantly more than females, and females in the Coastal study area used platforms significantly more (14.3%) than females in the Sierra study area (5.9%; χ^2 = 9.64, P = 0.046).

Resting-site Habitat Characteristics

Univariate Vegetation Analyses.—Initial variable reduction resulted in the retention of 5 topographic, 3 vegetation type, 11 tree abundance, 2 canopy closure, 10 tree size, and 4 ground-cover variables (Table 2). Using the data from focal and non-focal individuals, resting sites had significantly larger maximum dbh, average canopy closure, and shrub canopy closure, more large snags, and steeper slope than random sites. Resting sites also had significantly more variable tree dbhs and significantly less variable canopy closures (Table 3). Conifers and hardwoods were smallest at random sites, larger at resting sites, and largest when used as resting structures (Fig. 2). The 2 study areas differed in respect to the variables that were significantly different at rest and random sites, and in respect to the characteristics of the sites used for resting (Table 3). Most resting and random sites at both study areas were in the Dense CWHR canopy category (>60% canopy closure). Tree size class 5 (>61.0-cm dbh) was the

most frequent tree size class at resting sites in the Coastal area, whereas class 4 (28.0–61.0 cm) was the most frequent class in the Sierra. We found no conspicuous differences in CWHR tree size class among site types in either study area. All measures of basal area and the frequency of large snags were greater at resting sites used by females compared to males, though the tree dbh was similar (Table 3).

Resource Selection Functions

Only data from focal animals were used to estimate RSFs. This included 21 animals (6 M, 15 F; 9 and 12 from the Coastal and Sierra areas, respectively), although 1 female from the Sierra area was dropped from consideration due to complete separation of data points. Twelve variables were candidates for inclusion in the 4 selected RSFs (BA_LARGE, BA_SMALL, BACON, BAHDW, BARS, CANAVE, CANSTD, DBHMAX, DBHSTD, DBHAVE, DBHAVEH, SLOPE, WATER, CONSNAG; see Table 2 for definitions).

Fisher Models.—A single model accounted for >0.90 of the Akaike weight (Table 4) and took the form:

$$W(x) = \exp(0.0618 * \text{CANAVE} + 0.0153 * \text{DBHMAX} + 0.0229 * \text{SLOPE}).$$

This function indicates that fishers in California select sites with denser canopies, a larger maximum tree size, and steeper slopes (Tables 4, 5). Predictive power was moderate (R^2 = 0.31), and overall resting habitat use patterns varied considerably among individuals, but the concentration of Akaike weight suggests that resting habitat use by our study animals is influenced by a relatively simple combination of 3 variables that include biotic and abiotic features.

Coastal Models.—A single model accounted for >0.90 of the Akaike weight (Table 4) and took the form:

$$W(x) = \exp(0.06496 * \text{CANAVE} + 0.01437 * \text{DBHMAX} + 0.8692 * \text{CONSNAG}).$$

Resting sites in the Coastal study area were best distinguished from random sites on the basis of greater canopy closure, larger maximum tree size, and the presence of at least 1 large (>102-cm dbh) conifer snag (Tables 4, 5). Inclusion of the conifer snag variable distinguished the top Coastal model from the top Fisher model. The next most competitive Coastal models (ΔAIC_c = 5.92 and 7.44, respectively) included the variables

Table 2. Definitions and acronyms for variables recorded at resting structures and random sites within fisher home ranges in the Coastal (Six Rivers National Forest) and Sierra (Sequoia National Forest) study areas during May 1993–Sep 1997 and Apr 1994–Oct 1996, respectively.

Variable	Acronym	Measurement technique / definition
Topographic variables		
Percent slope	SLOPE	Clinometer; average of uphill and downhill
Elevation	ELEV	Altimeter (m)
Topographic position	TOPOG	Estimated: ridge, mid or drainage
Aspect	A	Compass
Distance to water	WATER	< or > 100 m
Vegetation cover type variables		
CWHR ^a habitat type	CWHRTYPE	Estimating using CWHR guide
CWHR habitat size class	CWHRSIZE	Estimating using CWHR guide
CWHR canopy closure	CWHRCC	Estimating using CWHR guide
Tree abundance variables		
Total basal area	BA	20-factor prism (m ² /ha)
Basal area large trees	BA_LARGE	m ² /ha of trees > 52 cm dbh ^b
Basal area small trees	BA_SMALL	m ² /ha of trees ≤ 51 cm dbh
Basal area trees >102-cm dbh	BA5	m ² /ha of trees >102-cm dbh
Basal area conifers	BACON	m ² /ha of conifers
Basal area large conifers	BACONL	m ² /ha of conifers >52-cm dbh
Basal area small conifers	BACONS	m ² /ha of conifers ≤51-cm dbh
Basal area hardwoods	BAHDW	m ² /ha of hardwoods
Basal area live trees	BALIVE	m ² /ha of non-snags
Basal area resting-site sized trees	BARS	Sierra: m ² /ha of hardwoods >42-cm dbh and conifers >72-cm dbh; Coastal: m ² /ha of hardwoods >56-cm dbh and conifers >79-cm dbh
Basal area snags	BASNAG	m ² /ha of standing dead trees
Canopy closure variables		
Average canopy closure	CANAVE	Mean of densiometer readings at 5 plot locations
Canopy closure standard deviation	CANSTD	Standard deviation of densiometer readings at 5 plot locations
Tree size variables		
Average conifer dbh	DBHAVEC	Mean dbh (cm) of conifers in the prism sample
Average hardwood dbh	DBHAVEH	Mean dbh (cm) of hardwoods in the prism sample
Average dbh	DBHAVE	Mean dbh (cm) of all trees in the prism sample
Maximum dbh	DBHMAX	Dbh (cm) of the tree with the largest dbh on the plot; including the resting structure
Conifer quadratic mean dbh	DBHQMC	Quadratic mean diameter (cm) of conifers
Quadratic mean dbh	DBHQM	Quadratic mean diameter (cm)
Standard deviation dbh	DBHSTD	Standard deviation of mean dbh (cm)
Average tree height	TRHTAVE	Mean height (m) of trees in the prism sample
Tree height standard deviation	TRHTSTD	Standard deviation of height (m) of trees in the prism sample
Presence large conifer snag	CONSNAG	Presence of ≥1 conifer snag >102-cm dbh
Ground cover variables		
Number of logs	NOLOGS	Number of logs >15-cm diameter at smallest end
Number of large logs	NOLOGS_L	Number of logs >60-cm diameter at smallest end
Number of small logs	NOLOGS_S	Number of logs >15-cm diameter and <30-cm diameter at smallest end
Estimated shrub cover	SHRUBCC	Observer estimated percent shrub cover

^a CWHR = California Wildlife Habitat Relationships.

^b dbh = diameter at breast height.

slope and water, reinforcing the influence of topographic features on resting-site use.

Sierra Models.—No single model accounted for >0.90 of the Akaike weight so we averaged the 2 models that together accounted for >0.90 of the weight (Table 4). This resulted in a model that took the form:

$$W(x) = \exp(0.0149 \cdot \text{DBHMAX} + 0.0301 \cdot \text{DBHSTD} + 0.0194 \cdot \text{SLOPE} + 0.7663 \cdot \text{WATER}).$$

Vegetation structure was represented in the model by the maximum and standard deviation of tree dbh, whereas slope and the presence of water within 100 m indicated the role of topography in explaining resting-site selection in the southern Sierra Nevada (Tables 4, 5). Topographic variables would appear to be important because slope and water were both represented in each of the models that were averaged. Unique to the Sierra models, also, was the frequency with which

Table 3. Select habitat characteristics for resting and random sites for fishers studied in the Coastal (Six Rivers National Forest, California, USA, May 1993–Sep1997) and Sierra (Sequoia National Forest, California, USA, Apr 1994–Oct 1996) study areas. Summary statistics calculated based on mean values for 15–20 observations/individual fisher ($n = 21$ fishers). An asterisk after mean values in the random column indicates that the variable is statistically different than the mean resting value. T -tests ($\alpha < 0.0033$; 0.05/13 variables) were used for the continuous variables and chi-square tests for the categorical variables.

Variable	Pooling	No. of fishers	Resting		Random	
			Mean	SD	Mean	SD
Continuous						
Basal area (m ² /ha)	All	21	65.8	11.58	59.9	8.60
	Female	15	69.0	9.72	61.3	9.02
	Male	6	58.0	13.01	56.4	6.89
	Coastal	9	71.9	11.76	57.8	10.09
Conifer basal area (m ² /ha)	Sierra	12	61.3	9.53	61.5	7.37
	All	21	51.2	11.79	45.6	10.96
	Female	15	53.9	12.37	45.4	11.53
	Male	6	44.4	7.14	46.2	10.37
Hardwood basal area (m ² /ha)	Coastal	9	55.5	14.53	42.1	9.74
	Sierra	12	48.0	8.54	48.2	11.48
	All	21	14.5	6.74	14.1	6.82
	Female	15	14.8	6.91	15.7	7.20
Average dbh (cm)	Male	6	13.6	6.84	10.0	3.67
	Coastal	9	16.0	5.68	15.2	5.88
	Sierra	12	13.3	7.48	13.2	7.59
	All	21	62.9	12.54	56.3	9.94
Maximum dbh (cm)	Female	15	62.4	12.71	54.4	10.61
	Male	6	64.2	13.19	61.1	6.49
	Coastal	9	70.7	8.97	61.2	9.74
	Sierra	12	57.2	11.93	52.7	8.78
Average canopy closure (%)	All	21	131.2	22.58	111.0*	15.89
	Female	15	132.3	25.45	110.1*	17.65
	Male	6	128.3	14.58	113.3	11.35
	Coastal	9	147.7	18.20	119.1*	14.76
Slope (%)	Sierra	12	118.8	17.20	104.9*	14.35
	All	21	93.4	5.07	88.8*	5.45
	Female	15	94.7	1.63	90.3*	3.77
	Male	6	90.1	8.79	85.0	7.41
Slope (%)	Coastal	9	95.0	1.62	86.7	7.29
	Sierra	12	92.1	6.40	90.3	3.03
	All	21	49.8	8.25	42.6*	6.87
	Female	15	49.0	8.78	42.4	7.64
Basal area small trees (m ² /ha)	Male	6	51.9	6.94	43.0	5.02
	Coastal	9	47.4	8.66	42.8	7.16
	Sierra	12	51.5	7.82	42.4	6.97
	All	21	33.4	9.54	32.78	10.03
Basal area large trees (m ² /ha)	Female	15	34.6	7.91	35.30	10.04
	Male	6	30.5	13.25	26.46	7.28
	Coastal	9	30.4	5.10	27.58	9.54
	Sierra	12	35.6	11.57	36.67	8.84
Basal area snags (m ² /ha)	All	21	19.5	6.69	18.43	4.80
	Female	15	20.3	6.94	17.98	5.27
	Male	6	17.6	6.13	19.56	3.53
	Coastal	9	23.6	6.85	19.87	5.72
Standard deviation	Sierra	12	16.5	4.84	17.36	3.90
	All	21	10.0	3.08	8.66	2.51
	Female	15	10.9	2.98	8.70	2.86
	Male	6	7.9	2.38	8.54	1.50
Standard deviation	Coastal	9	9.3	2.60	6.89	2.16
	Sierra	12	10.5	3.43	9.98	1.89
	All	21	36.0	7.03	29.58*	4.64
	Female	15	36.5	7.75	29.33*	5.32

Table 3. continued.

Variable	Pooling	No. of Fishers	Resting		Random	
			Mean	SD	Mean	SD
dbh	Male	6	34.6	5.11	30.22	2.50
	Coastal	9	40.5	3.75	32.06*	4.60
	Sierra	12	32.6	7.07	27.72	3.87
Standard	All	21	6.0	3.00	8.07*	1.94
deviation	Female	15	5.1	1.28	7.95*	2.05
canopy	Male	6	8.3	4.76	8.34	1.76
	Coastal	9	4.7	1.16	8.74*	2.47
	Sierra	12	7.0	3.58	7.56	1.32
Shrub	All	21	15.0	9.30	27.15*	10.05
canopy	Female	15	14.0	9.55	26.95*	11.31
closure	Male	6	17.5	8.93	27.65	6.71
	Coastal	9	15.8	9.85	28.07	8.35
	Sierra	12	14.3	9.25	26.47*	11.48
Categorical			Resting		Random	
	Pooling		<i>n</i>	%	<i>n</i>	%
Presence of large (>102cm dbh) conifer snags (percent of sites)						
	All		452	40.9	382	23.8*
	Female		332	45.8	285	22.5*
	Male		120	27.5	97	27.8
	Coastal		176	47.2	188	22.8*
	Sierra		276	36.9	194	24.7*
Presence of water within 100 m (percent of sites)						
	All		452	48.4	385	35.1*
	Female		332	50.6	288	32.6*
	Male		120	42.5	97	42.3
	Coastal		176	44.3	191	42.2
	Sierra		276	51.9	194	27.8*

the average dbh of hardwoods (DBHAVEH) appeared in the candidate models (22 of 24 models). This variable was not included in the top model, however, because it did not appear in either of the 2 models that were averaged.

Female Models.—A single model accounted for >0.90 of the Akaike weight (Table 4) and took the form:

$$W(x) = \exp(0.0743 \cdot \text{CANAVE} + 0.0138 \cdot \text{DBHMAX} + 0.0263 \cdot \text{SLOPE} + 0.8923 \cdot \text{CONSNA})$$

Female fishers selected resting sites that had denser canopies, larger trees, were on steeper slopes, and included large conifer snags compared to random sites within their home ranges (Tables 4, 5). The next most competitive model ($\Delta\text{AIC}_c = 5.56$) included the same variables, except that the presence of a large conifer snag was excluded.

Model Performance.—We evaluated the top RSFs using data from 84 resting sites and 22 random sites that were not used to develop the models. The models were reasonably effective at distinguishing known resting sites from random sites,

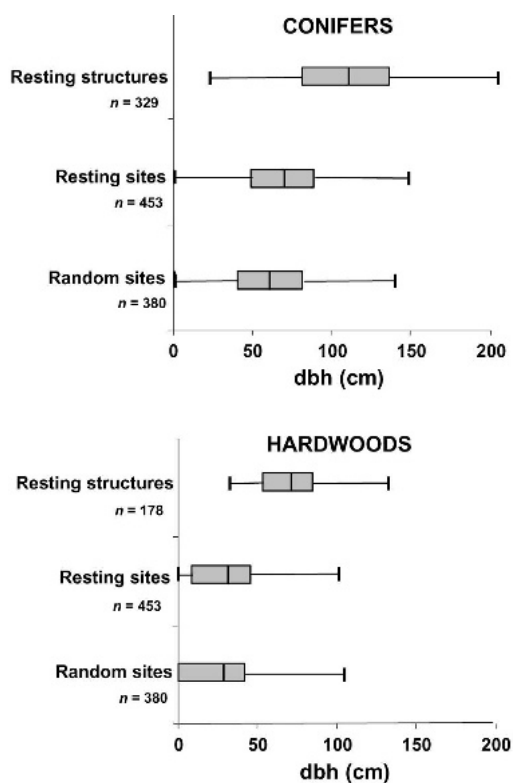


Fig. 2. Box plots for the diameter at breast height (dbh; cm) for conifers and hardwoods at random sites and at resting sites, and resting structures used by fishers in California, USA, 1993–1997. The vertical line in the middle of the box marks the median or 50th percentile. The top and bottom edges mark the quartiles, or the 25th and 75th percentiles. The “whiskers” extend from the quartiles to the farthest observation within 1.5 times the distance between the quartiles.

despite the small sample of random-site test data available (Fig. 3). In each set of models, the predicted values for the random sites were always distributed at lower values than the resting sites, and few random points had scaled relative probabilities of selection that exceeded 0.80. Importantly, the distribution of predicted values at resting sites was skewed toward values >0.60 for all models except the Sierra (Fig. 3).

DISCUSSION

Our results address several levels of habitat selection made by adult fishers after they have chosen a home range. Resting-habitat selection involves the choice of resting structures within stands as well as the vegetation and topographic characteristics in the vicinity of the structure, the resting site. Our study provides a unique opportunity to understand the influence of geographic location on

resting-habitat selection because a similar number of fishers were studied at each area, using identical methods applied over the same period.

Resting-structure Use

Most resting structures at both of our study areas were in standing trees, and most of these were large ($\bar{x} > 100$ -cm dbh). Trees used as resting structures were much larger than the average available tree, suggesting that fishers prefer to rest in the largest trees or snags available. This behavior is similar to that reported for fishers elsewhere in western North America, where cavities in large live and standing dead trees also are used for resting (Buck et al. 1983, Weir and Harestad 2003). Although logs were used less frequently, they too were of the largest size class available, averaging 123-cm diameter at the large end. Despite that most resting structures were relatively large, we recorded instances when fishers rested in trees and logs with relatively small diameters, indicating that large diameter may not be an absolute requirement for a resting structure.

The species of tree used appeared to be less important than its structural characteristics; tree species that decay to form cavities in the bole are more important for resting than those that do not. We did not estimate ages of resting trees, but trees must be large and old to decay to the point in which cavities useful to fishers will form. In unmanaged stands, white firs and Douglas-firs >100 -cm dbh, for example, usually are 150–200 years old (Schumacher 1930, Hann and Larsen 1990). Fishers frequently used hardwoods, especially black oaks, as rest structures in the Sierra study area. In this respect, fishers in the Sierra Nevada resemble fishers in eastern and midwestern North America. Hardwoods comprised 40% of maternal den structures in the northeastern United States (Powell et al. 1997), 94% of natal dens in Maine (Paragi et al. 1996), and about 90% of resting sites in Wisconsin (Kohn et al. 1993).

Fishers not only used the largest woody structures for resting bouts, but they also used numerous structures. Our observation that individual resting structures were rarely reused is similar to that reported elsewhere (Kilpatrick and Rego 1994, Seglund 1995) and suggests that fishers do not restrict use of their home range to a few central locations but instead require multiple resting structures distributed throughout their home ranges. Martens forage over portions of their home range sequentially, resting in trees and snags close to their foraging areas and most

Table 4. Summed Akaike's Information Criterion (ΣAIC_c) values for individual fishers, the range of AIC_c values for individual fishers, ΔAIC_c , Akaike weights (w_i), and maximum rescaled R^2 values for top resource selection functions for each of 4 resting-site habitat models developed from data collected in California from 1993 to 1997. The Fisher model includes all focal individuals of both sexes in both study areas, the Coastal model includes only focal animals from northwestern California, the Sierra model includes focal animals from the southern Sierra Nevada, and the Female model includes focal females from both study areas. Twenty-one candidate models were originally evaluated for each set of data. In addition to the top model, the next most competitive models are included if they account for at least 0.01 Akaike weight.

Models ^a	No. of fishers	AIC _c range		ΣAIC_c	ΔAIC_c	w_i	R^2	
		Min	Max				Mean	SE
Fisher								
CANAVE, DBHMAX, SLOPE	20	29.12	77.93	955.72	0.00	1.00	0.31	0.04
Coastal								
CANAVE, DBHMAX, CONSNAG	9	36.46	62.74	410.95	0.00	0.92	0.35	0.06
CANSTD, DBHMAX, SLOPE	9	33.87	64.63	416.87	5.92	0.05	0.33	0.07
CANAVE, DBHMAX, SLOPE, CONSNAG	9	36.79	65.21	418.39	7.44	0.02	0.39	0.07
Sierra								
DBHMAX, SLOPE, WATER	11	30.52	78.74	555.20	0.00	0.51	0.25	0.05
DBHSTD, SLOPE, WATER	11	32.26	78.25	555.32	0.12	0.48	0.25	0.06
DBHMAX, DBHAVEH, WATER	11	31.69	78.91	562.44	7.24	0.01	0.24	0.04
Female								
CANAVE, DBHMAX, SLOPE, CONSNAG	14	36.79	76.58	709.19	0.00	0.93	0.35	0.05
CANAVE, SLOPE, CONSNAG	14	34.10	75.70	714.76	5.56	0.06	0.26	0.05

^a Parameter definitions are given in Table 2.

recent kill sites (Marshall 1951, Spencer 1981). The pattern of resting-site use by fishers indicates that they do the same, and the low reuse rate of individual structures may be influenced by the need to minimize transit time between kill sites and a resting location.

Females favored resting structures that were more enclosed and appeared to provide the greatest security (i.e., live trees and snags). Males used the same types of resting structures as females but in different proportions, distributing their resting more evenly over a greater variety of structure types. The greater use of standing trees by females might be expected during the breeding and kit-rearing season when females need to protect themselves and their young from predators or to control access by males. However, the phenome-

non occurred year-round and is similar to the preference by female European pine martens (*Martes martes*) for cavities compared to other resting-structure types (Zalewski 1997) and to the apparent preference by female fishers for smaller, more secure, cavities than chosen by male fishers (Kilpatrick and Rego 1994). Females, being substantially smaller, may place a premium on protection from predators and on protection from thermal and moisture extremes. Alternatively, selection for cavities as natal dens (Paragi et al. 1996) may predispose females to choosing similar features as resting structures throughout the year.

Resting-site Habitat Selection

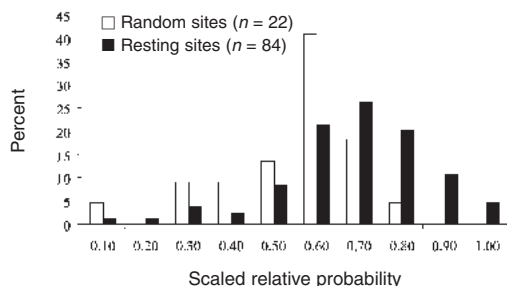
Although the resting structure is presumably the primary attractant, our analysis revealed that

Table 5. Average parameter estimates and standard errors for fisher resting-site selection analysis. The Fisher model includes all focal individuals of both sexes in both study areas, the Coastal model includes only focal animals from northwestern California, the Sierra model includes focal animals from the southern Sierra Nevada, and the Female model includes focal females from both study areas (1993–1997). Averages are pooled across individuals and weighted by 1/Standard Error for the individual values. The sample size (n) refers to the number of focal animals.

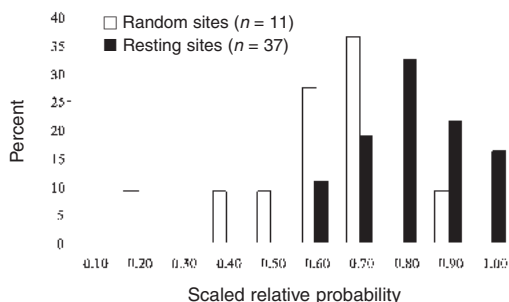
Model	n	Parameter ^a											
		CANAVE		DBHMAX		DBHSTD		SLOPE		WATER		CONSNAG	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Fisher	20	0.0618	0.0129	0.0153	0.0030			0.0229	0.0054				
Coastal	9	0.0649	0.0196	0.0143	0.0046							0.8692	0.3392
Sierra	11			0.0149	0.0044	0.0301	0.0111	0.0194	0.0069	0.7663	0.2719		
Female	14	0.0743	0.0174	0.0138	0.0040			0.0263	0.0069			0.8923	0.2693

^a Parameter notation: CANAVE = Mean of densiometer readings at 5 plot locations; DBHMAX = diameter at breast height (dbh; cm) of the tree with the largest dbh on the plot; DBHSTD = standard deviation of mean dbh (cm); SLOPE = average of uphill and downhill measured by clinometer; WATER = water < or > 100 m from site; CONSAG = presence of ≥ 1 conifer snag >102-cm dbh.

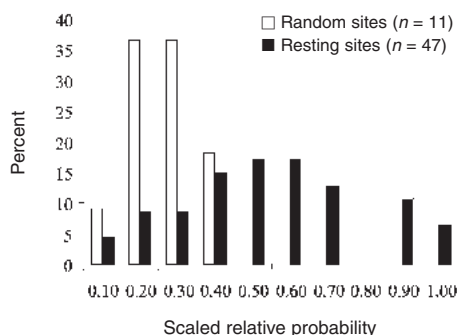
(a) Fisher model—test data



(b) Coastal model—test data



(c) Sierra model—test data



(d) Female model—test data

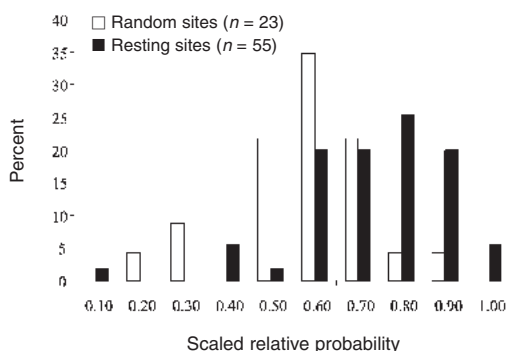


Fig. 3. Predicted relative probability histograms for independent data evaluated using selected models describing fisher resting locations in California, USA, 1993–1997. (a) Fisher model; (b) Coastal model; (c) Sierra model; (d) Female model. Data for all observations were rescaled such that the maximum relative predicted probability of use assumed a value of 1.00.

numerous associated environmental features are related to the selection of a resting location. The final models for data pooled from both study areas and sexes (the Fisher model) indicated that combinations of vegetation and topographic features contribute to resting-site selection. Maximum tree dbh, canopy closure, and slope accounted for >0.90 of the Akaike weight in the final Fisher model; a good indication of the importance of these 3 parameters. Despite the fact that random sites were prejudiced toward the inclusion of larger trees and denser canopies (because each usually was centered on a large tree or snag), the sites selected for resting had even larger trees and denser canopies than random sites. The RSFs and the univariate analyses collectively indicate that fishers select areas as resting sites where structural features (e.g., tree bole size) are most variable but where canopy cover is least variable. This suggests that resting fishers place a premium on continuous overhead cover, as reported previously (Buck et al. 1994, Jones and Garton 1994, Klug 1996, Carroll et al.

1999), but prefer resting locations that also have a diversity of sizes and types of structural elements. Resting-site choice by females was influenced by a combination of vegetation and topographic features including canopy closure, maximum tree dbh, slope, and large conifer snags. Resting structures occurred where slopes were steep, regardless of which subset of animals was considered. Importantly, the predictive power of all our models, as indicated by the generalized R^2 values (Table 4) was limited (range = 0.25–0.35), indicating that factors other than those measured in our study area influence the selection of resting sites by fishers.

A number of features that we expected to differ between used and random locations did not (e.g., CWHR cover types, size classes, densities), which may be related to understanding the hierarchical context of the analysis. By studying habitat selection at the within-home-range scale, we automatically guaranteed that all locations would be relatively similar because they (1) share spatial proximity, and (2) are within areas occupied by

fishers. We did not assess habitat selection at the landscape scale in this study, so areas unoccupied by fishers may differ substantially in CWHR type or other characteristics compared to those we reported.

Resting locations on the Coastal study area were best distinguished from random locations by a simple model including the maximum size of trees, dense canopies, and the presence of large conifer snags. The importance of hardwoods in the candidate models for the Sierra area, but not the Coastal area, probably is best explained by the importance of black oaks as resting structures in the Sierra Nevada. Tanoaks contribute much of the basal area of hardwoods in the Coastal study area but were rarely used as resting structures. This probably explains why no feature of hardwoods was included in candidate models for the Coastal area. Interestingly, the greater mean basal areas and dbhs at Coastal resting sites compared to Sierra resting sites were not as evident when these same features were compared at random sites at each study area (Table 3), which may reflect stronger selection for sites with large trees in the Coastal than the Sierra study area. The inclusion of standard deviation of tree dbh in the top Sierra model suggests a role for heterogeneity of forest structure at Sierra but not Coastal resting sites.

Distance to water was an important variable in the selected, and many of the candidate, models in the Sierra but not the Coastal study area. Fishers occur primarily in cool, moist, boreal forests in North America (Buskirk and Powell 1994, Gibilisco 1994). Fishers in the southern Sierra Nevada occur at the southern margin of their range, where the weather is hotter and drier than habitats in the north and east, and fishers may preferentially search for resting structures in microhabitats that are cool and damp. The importance of steep slopes, large trees, dense canopy, and the proximity to water may reflect this preference in the Sierra study area. The Coastal area, in the cooler and moister Pacific Northwest, does not share the extremes of temperature and moisture experienced by the fishers in the Sierra area.

At a larger scale, resting-site choices by fishers in both study areas may be influenced by the prolonged, hot and dry summers that characterize California's unique Mediterranean climate. This may help explain apparent differences in the association of fishers with mature/old-growth forests in the western and eastern parts of its

North American range. Most data in our study were collected during the dry season when the maximum temperature was $>33^{\circ}\text{C}$, the relative humidity was $<30\%$, almost all days were sunny, and rain was infrequent. The Sierra study area is warmer and drier than the Coastal area, but because the Coastal site is on the southern extreme of the Pacific Northwest, it too is routinely hotter and drier during the summer than the eastern portion of the fisher's range. The selection of structures with cavities and resting sites (especially in the Sierra) that mitigate the effects of heat and desiccation may be a result of the prolonged hot and dry season typical of Mediterranean climates. This may be key to 1 of the important differences noticed in fisher ecology between populations in the western United States and elsewhere. Perhaps fishers in the eastern United States find less need for protection from heat and water loss that cavities in old-growth trees provide because summer habitats are not subject to the persistent hot and dry conditions.

MANAGEMENT IMPLICATIONS

Because large trees had such a prominent influence on resting-site selection in each of the top models, managers can have direct effects on the resting habitat of fishers by favoring the retention and recruitment of trees that achieve the largest sizes possible. These are the trees that host most resting structures, and also characterize the vegetation near the structure. We discovered infrequent reuse of the same resting structure, which indicates that fishers use—and may require—many large trees, snags, and logs distributed within home ranges. The resting trees, and in many cases, the trees in their immediate vicinity were among the largest standing live and dead trees within fisher home ranges. The objective of recruiting and retaining large trees should not overshadow, however, the goal of encouraging structural diversity; standard deviation of dbh was included in the Sierra model. This observation suggests that developing stands that include variation in the size of trees may be beneficial. We agree with Weir and Harestad (2003) that the maintenance of large structural elements at small scales may mitigate for the negative effects of large-scale alterations of habitat. However, we cannot at this time recommend standards for the optimal distribution of resting-structure types across a landscape.

Management of fisher habitat also should consider both conifers and hardwoods. Hardwoods

are not as commonly exploited in California and less effort is expended to determine their abundance and condition. The importance of large hardwoods (particularly black oak) as resting habitat for fishers calls for greater effort to understand the ecological conditions that favor the maintenance of large and decadent black oaks in mixed-conifer stands. Black oaks regenerate best in open conditions after a disturbance (Pavlik *et al.* 1991) and appear to have declined during the era of fire exclusion (T. Jimerson, U.S. Forest Service, Six Rivers National Forest, personal communication).

Live trees and snags provide important refuge for wildlife; however, snags are almost always emphasized in discussions of important wildlife elements in forests (e.g., Neitro *et al.* 1985, Carey *et al.* 1997). Live trees receive less attention, yet for fishers, live trees are the most frequently used resting structure. Although large live trees were the most common resting structure (46.4%), dead woody structures (large snags and logs) were chosen for resting almost as frequently (44.5%). Care should be taken in the application of fire in fisher resting habitat because large snags are especially vulnerable to loss from prescribed fire (Horton and Mannan 1988). Large live trees are among the most slowly renewing elements of the forest and are dominant elements (Power *et al.* 1996) in forest communities. Conifers and hardwoods may take hundreds of years to develop the size and the decadence necessary to be used by fishers for resting. Because large live trees and large snags are less abundant in the Sierra Nevada and the Pacific Northwest than historically (McKelvey and Johnson 1992, U.S. Forest Service and U.S. Department of the Interior 1994, Bouldin 1999), every management activity designed to favor fishers should be evaluated as to whether it enhances or reduces the availability or development of large live and dead trees and large logs. Management actions that are designed to reduce fuels and the possibility of catastrophic fire and to treat tree diseases should be especially careful about protecting legacy or residual woody structures (Hunter and Bond 2001), as well as trees with mistletoe infections that are used by fishers for resting (Mazzoni 2002).

Our finding that fishers select sites with dense canopy cover is not novel (Buck *et al.* 1994, Jones and Garton 1994, Seglund 1995, Dark 1997, Carroll *et al.* 1999). Most RSFs achieved greatest values for high average canopy closures. The especially dense canopy and volume of small trees in

the Sierra area, in particular, increase the threat of severe fire and the response by management to this threat. If the response includes significant reduction in canopy or density of vegetation, it could affect the habitat value for fishers. However, canopy is relatively easy to provide because of contributions from the under, mid, and overstory and, unlike large woody structures, if canopy closure is reduced below an acceptable threshold it can recover relatively quickly.

Some features associated with fisher habitat are similar in both study areas, and one would not err to manage in both regions for large trees and dense canopies. For other characteristics, however, applying locally derived information is important. For example, drawing inference to the North Coast forests from studies in the southern Sierra Nevada would place unnecessary emphasis on the importance of nearby water and black oaks as resting structures and would erroneously interpret the importance of hardwoods as rationale for managing for tanoaks, a species that was not used by fishers as a resting structure in the Coastal area. Geographic variation in resting habitat has also been discovered in the European pine marten, which uses ground resting structures in northern Europe and cavities in trees or nests in the south (Zalewski 1997).

Our models also can be used to assess habitat and change in habitat condition. For example, the final pooled Fisher model included 3 variables that can be easily measured at sample locations in forest stands that are candidates for vegetation management. The relative predicted probability of use could then be estimated at plots by entering the parameter values in the RSF. The mean of these values could then in turn be used as a measure of the likelihood that the stand functions as potential fisher resting habitat. Furthermore, should a decision be made to treat the area, the stand could again be sampled to determine the change in relative predicted probability that resulted from the treatment. We plan additional work to test the RSFs we presented and to develop this application of our research.

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Appendix A. Sizes of hardwood, live conifer, conifer snag, platform and log resting structures used by fishers at the Coastal (Six Rivers National Forest) and Sierra Nevada (Sequoia National Forest) study areas during May 1993–Sep 1997 and Apr 1994–Oct 1996, respectively. Values are averaged over all (focal and non-focal) individuals. Size of hardwoods and conifers is measured at breast height (dbh); size of platform is the dbh of tree in which a nest, mistletoe growth, or witch's broom was used; size of log is its maximum diameter.

	No. of resting structures	No. of individ.	Mean (cm)	SD	Min. (cm)	Max. (cm)
Hardwood						
Total	178	31	69.0	24.7	30.0	149.0
Female	138	18	67.6	22.4	30.0	147.0
Male	40	13	73.6	31.2	30.0	149.0
Coastal	32	14	87.6	30.1	42.0	149.0
Sierra	146	17	64.9	21.4	30.0	145.0
Conifer-live						
Total	133	36	117.2	45.2	31.0	433.0
Female	98	23	118.3	45.8	35.0	433.0
Male	35	13	114.0	43.9	31.0	183.0
Coastal	64	19	124.7	37.8	35.0	205.0
Sierra	70	17	110.2	50.4	31.0	433.0
Conifer-snag						
Total	143	34	119.8	45.3	45.0	328.0
Female	115	22	121.3	47.2	50.0	328.0
Male	28	12	113.4	35.8	45.0	190.0
Coastal	50	16	119.0	32.7	66.0	200.0
Sierra	93	18	120.3	50.8	45.0	328.0
Platform						
Total	53	18	71.1	35.2	12.0	162.0
Female	31	10	77.6	37.2	12.0	162.0
Male	22	8	61.9	30.6	28.0	117.0
Coastal	35	11	68.1	37.4	12.0	162.0
Sierra	18	7	76.8	30.5	28.0	142.0
Log						
Total	43	21	123.0	84.1	45.0	500.0
Female	23	13	128.6	101.7	45.0	500.0
Male	20	8	116.6	59.9	60.0	260.0
Coastal	10	5	95.1	44.2	50.0	200.0
Sierra	33	16	131.5	91.7	45.0	500.0